

THE TAPHONOMY OF GOLDEN EAGLE PREY ACCUMULATIONS AT GREAT BASIN ROOSTS

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ABSTRACT.—Surface collections and limited excavations at Cathedral Roost in northern Utah retrieved hundreds of leporid bones accumulated by golden eagles (*Aquila chrysaetos*). These bones provide data for identifying golden eagle prey accumulations in archaeological and paleontological contexts. Jackrabbit (*Lepus* spp.) bones dominate the assemblage and are represented predominantly by posterior body parts, especially tibiae and hind feet. Evidence of bone attrition inflicted by eagle feeding is rare and indicates that skeletal damage alone will seldom prove useful in identifying prey remains accumulated at nest sites. However, the data suggest that combined consideration of taxonomic presences, skeletal element completeness, and body part representation can be used to distinguish eagle-produced bone accumulations associated with nests and perches. Comparison of the Cathedral Roost prey assemblage with leporid remains collected recently from a golden eagle roost in western Nevada reveals marked similarities in taxonomic and skeletal composition. Leporid skeletal frequencies and completeness in golden eagle nest accumulations will often be different than those produced by other Great Basin predators, including humans.

RESUMEN.—Las colectas de superficie y excavaciones limitadas en Cathedral Roost en el norte del estado de Utah, en los Estados Unidos de Norteamérica, produjeron cientos de huesos de lepóridos acumulados por águilas doradas (*Aquila chrysaetos*). Estos huesos proporcionan datos para identificar las acumulaciones de presas de águilas doradas en contextos arqueológicos y paleontológicos. Los huesos de liebre (*Lepus* spp.) dominan el conjunto y están representados predominantemente por las partes traseras del cuerpo, especialmente tibias y pies traseros. Es rara la evidencia de desgaste de los huesos ocasionado por las águilas al alimentarse, lo cual indica que el daño esquelético por sí solo pocas veces será útil para identificar restos de presas acumulados en sitios de anidamiento. Sin embargo, los datos sugieren que una consideración combinada de presencias taxonómicas, integridad de elementos esqueléticos, y representación de partes del cuerpo puede ser usada para distinguir acumulaciones de huesos producidos por águilas, asociadas con nidos y perchas. La comparación del conjunto de restos de presas de Cathedral roost con restos de lepóridos recolectados recientemente en un lugar de anidamiento de águilas doradas en el occidente del estado de Nevada revela semejanzas marcadas en la composición taxonómica y esquelética. La frecuencia e integridad de los esqueletos de lepóridos en las acumulaciones asociadas con nidos de águilas doradas frecuentemente serán diferentes de aquéllas producidas por otros depredadores, in-

cluyendo los humanos, en la zona de la Gran Cuenca del occidente de los Estados Unidos.

RÉSUMÉ.—Des collections de surface et des excavations limitées menées à Cathedral Roost dans le nord de l'Utah ont permis de découvrir des centaines d'ossements de léporidés accumulés par des aigles royaux (*Aquila chrysaetos*). Ces ossements fournissent des données pour identifier les accumulations de proies de l'aigle royal dans des contextes archéologiques et paléontologiques. Les ossements du gros lièvre américain (*Lepus* spp.) dominant l'assemblage et ils sont représentés principalement par les parties postérieures du corps, surtout les tibias et les pattes arrière. Il y a peu d'évidence d'attrition des os occasionnée par l'alimentation des aigles et les dommages squelettiques à eux seuls ne pourront donc que rarement servir à l'identification des restes de proie accumulés sur les sites des nids. Cependant, les données suggèrent que les présences taxinomiques, l'état complet ou non du squelette et la représentation des parties corporelles peuvent, considérés dans leur ensemble, servir à distinguer les accumulations des ossements produites par les aigles associées aux nids et aux perchoirs. La comparaison de l'assemblage de proies du site de Cathedral Roost avec des restes de léporidés d'un perchoir d'aigle royal dans l'ouest du Nevada révèle des similarités marquées en ce qui concerne les compositions squelettique et taxinomique. Les fréquences et l'état des squelettes de léporidés montreront souvent une différence suivant qu'ils proviennent des accumulations des nids d'aigles royaux ou des restes produits par d'autres prédateurs du Grand Bassin, y compris l'être humain.

INTRODUCTION

Jackrabbits (*Lepus* spp.) and cottontails (*Sylvilagus* spp.) are familiar inhabitants of a variety of Great Basin environmental contexts (Durrant 1952; Hall 1946, 1981). Due to their abundance, body size, and behavior, they constitute an integral portion of the diet of most local avian and terrestrial predators. Similarly, prehistoric and ethnographically known peoples in the region commonly exploited hares and cottontails for a variety of resources. A number of Great Basin ethnographic accounts describe hunting and carcass processing techniques (Fowler 1989; Steward 1938, 1941; Stewart 1942), and regional archaeofaunas commonly contain abundant leporid remains, as well as clothing, tools, and adornment manufactured from leporid fur and bone (Aikens 1970; Dansie 1987; Grayson 1988, 1990; Hockett 1993, 1994; Marwitt 1968; Schmitt 1990; Schmitt and Lupo 1995; Thomas 1983). The recovery of leporid bone tools offers definitive evidence of human modification. However, the identification of bone refuse generated by human subsistence activities is an arduous task because the bones of leporids and similarly-sized taxa usually lack the cut marks and flake scars often found on the remains of larger mammals (Gifford 1981; Lyman 1982, 1994a). Many of the leporid bones recovered from Great Basin sites probably represent human subsistence refuse, but raptorial birds and carnivorous mammals are capable of introducing leporid and other small animal remains into both open and sheltered archaeological deposits (Andrews 1990; Fernandez-Jalvo and Andrews 1992; Hockett 1989, 1991; Klippel *et al.* 1987; Schmitt and Juell 1994; Stiner 1994). Thus, the mechanisms responsible for the accumulation of hare and rabbit bones often are ambiguous, regardless of the depositional context.

In this paper I present data on leporid bones accumulated by golden eagles

(*Aquila chrysaetos*) at a nest site in northern Utah. Body part frequencies and evidence of skeletal attrition are described. These data may facilitate investigations directed toward identifying raptor prey assemblages in paleontological sites (Andrews 1990, Hoffman 1988, Kusmer 1990, Mayhew 1977) and distinguishing human and non-human leporid accumulations in archaeological contexts (Hockett 1989, 1991, 1993; Schmitt and Juell 1994; Szuter 1991). I briefly discuss golden eagle behavior and food habits in western North America. The study site (Cathedral Roost) and field and laboratory methods are described, followed by quantitative data and qualitative observations on the recovered bone assemblage. The Cathedral Roost assemblage is compared with leporid remains from a golden eagle roost in western Nevada to investigate potential variability in prey composition and body part representation. Golden eagle prey accumulations are then compared with leporid assemblages produced by other Great Basin raptors and terrestrial predators, including humans.

GOLDEN EAGLE ECOLOGY AND FOOD HABITS

Golden eagles are currently widespread in North America, Eurasia, and parts of northern Africa. In western North America they winter and breed in a variety of habitats extending from the southern Alaska coast to the highlands of northern Mexico (Johnsgard 1990, Ryser 1985, Snyder and Snyder 1991). Golden eagles are common residents of Great Basin mountains and foothills, often utilizing intermontane valleys for hunting (Edwards 1969, Ryser 1985, Smith 1971). Most golden eagle nests in the Great Basin are situated atop elevated ledges along cliffs or canyon walls (Smith 1971, Smith and Murphy 1982) where they roost singly or as mated pairs. Paired eagles often have several different nesting sites situated fairly close together and, "from year to year the birds may alternate sites, although one may be favored over the others" (Ryser 1985:240). Trees also may support nests (Cameron 1908, Hayward *et al.* 1976, Ryser 1985), but trees and similarly elevated natural and artificial structures more often serve as habitual perching sites used for resting, feeding, and/or evaluating hunting opportunities (Edwards 1969, Marion and Ryder 1977, Workman and Peterson 1989; see also Sugden 1928). Regardless of location, nest site selection appears to depend upon a number of factors, including inaccessibility (i.e., brood protection) and view of favorable foraging habitats (Smith and Murphy 1982).

Golden eagles are formidable diurnal raptors with wingspreads approaching 2.5 m (8 ft) and weights up to 4.8 kg (13 lbs) (Snyder and Snyder 1991:164). In a stoop these swift predators may reach speeds in excess of 300 km per hour (Ryser 1985). Small and medium-sized mammals constitute their principal prey, but golden eagles occasionally pursue other birds, fish, and reptiles, and scavenge carrion from medium and large mammal carcasses (Johnsgard 1990, Ryser 1985, Snyder and Snyder 1991). Records also exist for solitary and tandem attacks on larger mammalian taxa, including deer (*Odocoileus* spp.), pronghorn (*Antilocapra americana*), red fox (*Vulpes vulpes*), and coyote (*Canis latrans*) (Ford and Alcorn 1964, Johnsgard 1990, Lehti 1947).

Leporids (especially hares [*Lepus* spp.]) are the primary prey of golden eagles in the Great Basin and many other parts of North America (Edwards 1969, Mac-

Laren *et al.* 1988, McGahan 1968, Ryser 1985, Smith and Murphy 1979, Workman and Peterson 1989). Hunting techniques involve walking through low brush or, more commonly, observing prey movement from a perch and executing a series of low flights over vegetative cover to flush potential quarry. Golden eagle pairs occasionally hunt leporids cooperatively, with one driving the game from cover into the talons of the other (Ryser 1985:243). Once carcasses are obtained, the intestines are removed and discarded and the remaining soft organs are rapidly consumed. Flesh is then stripped and consumed along with a few bones that are eventually cast in pellets (Edwards 1969, Hockett n.d.). Golden eagles may consume most of their prey at the kill site, but they commonly transport whole carcasses or selected body parts to nests or favored perch sites for leisurely consumption. Variability in carcass/body part transport appears to be contingent upon the location of the kill site, competition with other predators, and whether or not a brood of chicks await food at the nest. Thus, golden eagles may produce scattered bone assemblages at open kill sites and/or bone concentrations below perches and nest sites (see also Hockett 1989). The presence of intact marrow cavities and adhering tissue in these bone concentrations attract other predators and scavengers (Edwards 1969: 101–102; see below). Consequently, bone assemblages originally produced by eagles are often rapidly affected by other taphonomic agents.

PROJECT SETTING AND METHODS

Investigations at Cathedral Roost were instigated as part of an interdisciplinary project focusing on paleoenvironmental change in the Bonneville Basin. The purpose of this project is to use data on non-human floral and faunal remains from regional packrat (*Neotoma* spp.) middens and dry caves in reconstructing environmental change over the past 15,000 years, and to investigate the processes behind those changes (Madsen 1994). In Homestead Cave on Homestead Knoll in the Lakeside Mountains of western Utah, excavation of a stratified 1 x 1 m column retrieved tens-of-thousands of small animal remains deposited primarily by avian predators. To investigate mechanisms responsible for fossil accumulations at the cave, bone assemblages produced by local predators were collected for comparison, including the golden eagle prey remains deposited at Cathedral Roost.

Cathedral Roost is situated on a steep, craggy limestone cliff on the northern tip of Homestead Knoll (Figure 1) approximately 1 km northwest of Homestead Cave. The site consists of two large nests located on narrow ledges approximately 10 m apart and 8 m from the ground surface at an elevation of 1,360 m. The nests afford a panoramic view of the Great Salt Lake and associated alkali flats to the north and northwest, and of vegetated hills and lowlands to the northeast. Modern vegetation in the region is a treeless desert scrub community dominated by greasewood (*Sarcobatus vermiculatus*), big sagebrush (*Artemisia tridentata*), shadscale (*Atriplex confertifolia*), and a variety of native and introduced grasses. Given site context and golden eagle home ranges in similar habitats (Smith 1971), the Cathedral Roost eagles probably procured most of their prey from vegetated valleys and ridges south and east of the roost (Figure 1). Golden eagles were observed at the roost and vicinity in 1992 and 1993, but none were observed while conducting field collections in July of 1994.

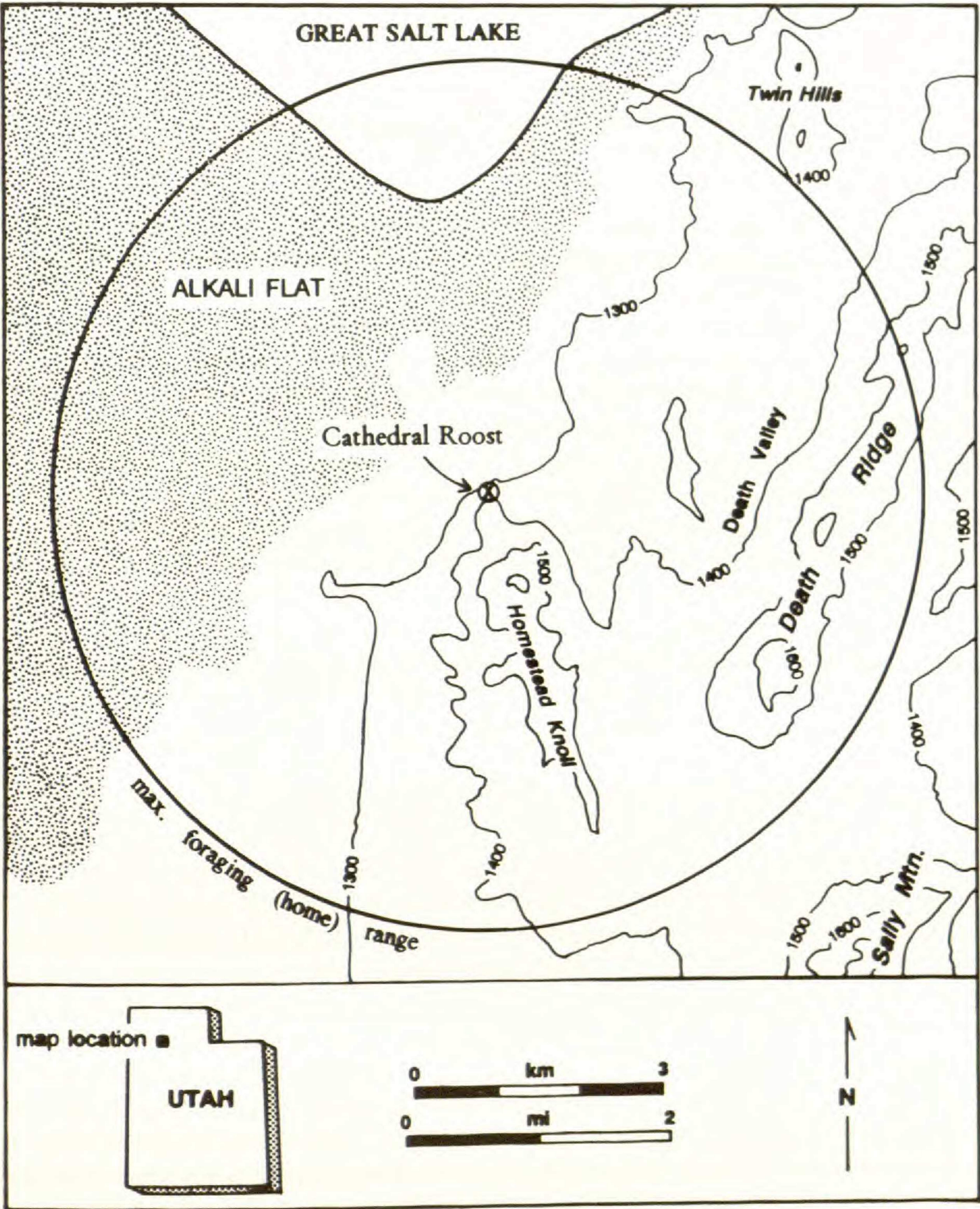


FIG. 1.—Location of Cathedral Roost in northwestern Utah. Golden eagle maximum home range is adopted from Smith (1971).

Abundant leporid bones littered approximately 5 x 20 m of the ground surface below the nests. Field investigations involved collection of all bones from the surface and shallow (5–10 cm) excavations of a ca. 1 x 2 m area below the westernmost nest. Excavated sediments were passed through 3.2 mm (1/8 in) mesh to extract a sample of small bones and bone fragments from the substrate. The majority of the bones were retrieved from surface collections; excavations yielded only a few iden-

tifiable leporid bones, five bird bones, and approximately 20 leporid-sized limb bone shaft fragments. Recovered bones were transported to the laboratory and sorted by taxon and skeletal element. No attempt was made to identify leporid species, but site context and reported modern taxonomic distributions in the region (Durrant 1952, Hall 1981) indicate that the specimens probably represent the black-tailed jackrabbit (*Lepus californicus*) and Nuttall's cottontail (*Sylvilagus nuttallii*) and/or the desert cottontail (*S. audubonii*). Average body weights for adult *L. californicus* and *S. nuttallii* are approximately 1.40 kg and 0.78 kg, respectively.

Bones were tallied by the number of identified specimens (NISP; Grayson 1984) per taxon, and minimum number of element (MNE) counts were derived by calculating the "minimum number of elements necessary to account for an assemblage of specimens of a particular skeletal element" (Lyman 1994b:289). Individual bones in articulated body segments were counted as single specimens. MNE values were derived with the intent of assessing the frequencies of skeletal element/body segment accumulations at the roost, and to appraise the extent of bone fragmentation by examining NISP to MNE ratios (see Lyman 1994b, 1994c). Based largely on the presence-absence of epiphyseal fusion, MNE calculations take into account the ontogenetic age of identified hare and cottontail specimens. Regardless of quantitative technique, *Lepus* remains dominate the assemblage, followed by *Sylvilagus* bones. Scant remains of a few additional taxa also were recovered, including three ground squirrel (*Spermophilus* spp.) bones, five articulated reptile (*Squamata*) vertebrae, and 14 bird bones representing at least two species.

LEPORID BODY PART FREQUENCIES AND SKELETAL ATTRITION

Surface collection and excavation retrieved 909 identified leporid specimens, with jackrabbits comprising the majority of the assemblage (Table 1). Most of the specimens are from adults, but a few subadult (i.e., unfused) jackrabbit and cottontail bones were collected. The most salient aspect of the assemblage is the high frequency of *Lepus* posterior body parts, indicating that these relatively meaty portions were preferentially transported to the roost. In the assemblage of paired elements, tibiae are most abundant followed by femora and calcanei. Astragali are relatively common, but given their small size I suspect that some additional specimens (as well as a few calcanei) passed undetected during surface collections. Innominates also are abundant, suggesting that hind quarters may often have been transported to the roost in articulated segments (Hockett 1993, Schmitt 1994). Scapulae appear to have been brought to the roost on rare occasions, as were front limbs and skulls.

While the majority of the leporid remains are incomplete (Table 2), much of the fragmentation resulted from post-depositional weathering. Most specimens are bleached and exhibit bone loss in the form of exfoliation, and many limb bones display longitudinal breakage as a result of split-line cracking (Behrensmeyer 1978, Tappen 1969; see also Hockett 1989). In several cases fragments of splintered limb bones were discovered *in situ* as conjoining pieces of the same weathered bone, and therefore were tallied as complete specimens. Although breakage largely consists of split-line cracking, a few specimens possess jagged, transverse breaks that probably were produced by eagles. Given the frequency and extent of the former,

TABLE 1.—Jackrabbit and cottontail remains collected from Cathedral Roost, Utah.

Element	NISP	<i>Lepus</i>		NISP	<i>Sylvilagus</i>		Total
		NISP	MNE		NISP	MNE	
		Unfused			Unfused		MNE
Cranium	12	0	5	2	0	1	6
Mandible	11	0	11	5	0	4	15
Scapula	5	0	4	2	0	2	6
Humerus	22	3	17	2	0	2	19
Radius	17	1	13	1	1	1	14
Ulna	11	0	11	0	0	0	11
Vertebra*	88	18	—	8	2	—	—
Rib	11	0	—	0	0	—	—
Innominate	39	7	36	4	0	4	40
Sacrum	15	4	15	1	0	1	16
Femur	62	16	47	3	1	3	50
Patella	7	0	7	1	0	1	8
Tibia	98	22	71	8	5	7	78
Astragalus	26	0	26	1	0	1	27
Calcaneus	48	0	48	2	0	2	50
Carpal/Tars.	39	0	—	3	0	—	—
Metapodial	183	27	—	11	1	—	—
Phalange	158	17	—	3	1	—	—
Totals	852	115	311	57	11	29	340

*Most (70%) are lumbar vertebrae.

the proportions of complete bones have been reduced. Golden eagles customarily discard complete bones, often in articulated body segments (Hockett 1993; see below), and I suspect that some of the interdependence of skeletal parts reflects post-depositional weathering. As a result, even though the calculated limb bone ratios are relatively low (Table 2), many of the NISP:MNE values have been inflated and all should be appraised as maximum ratios.

The leporid bones also exhibit damage resulting from rodent gnawing, predator digestion, and possible carnivore scavenging. Partially digested bone could have been deposited in pellets cast by golden eagles and/or carnivore scats; no intact pellets were discovered below the roost, but a single partially disaggregated coyote scat was observed. Most of the digestive corrosion is pronounced, often resulting in substantial bone disintegration similar to bones passed by mammalian carnivores. A number of taphonomic studies note that terrestrial carnivore digestion usually mars bone more extensively than raptor digestion given the high acidic constitution of gastric juices and because digestion takes place in both the stomach and intestines of mammalian predators (Andrews and Evans 1983, Rensberger and Krentz 1988). However, a number of factors are capable of causing inter-predator overlap in the extent of digestive corrosion (notably variability in the duration of digestion; Rensberger and Krentz 1988) and recent research has found that eagle digestion also corrodes bone extensively (Hockett n.d.). Thus, many of the Cathedral

TABLE 2.—Number and proportion of whole bones and NISP:MNE ratios of leporid remains from Cathedral Roost.

Element	<i>Lepus</i>			<i>Sylvilagus</i>			Total
	NISP Whole	% NISP Whole	NISP:MNE ^a	NISP Whole	% NISP Whole	NISP:MNE ^a	
Cranium	0	0	2.40	0	0	2.00	2.33
Mandible	0	0	1.00	0	0	1.25	1.07
Scapula	0	0	1.25	0	0	1.00	1.17
Humerus	7	31.8	1.50	0	0	1.00	1.42
Radius	7	41.2	1.67	1	100.0	1.00	1.55
Ulna	3	27.3	1.00	—	—	—	1.00
Innominate	4	10.3	1.09	1	25.0	1.00	1.09
Sacrum	3	20.0	1.00	1	100.0	1.00	1.00
Femur	21	33.9	1.58	1	33.3	1.00	1.54
Tibia	24	24.5	1.57	4	50.0	1.33	1.56
Astragalus	26	100.0	1.00	1	100.0	1.00	1.00
Calcaneus	44	91.7	1.00	1	50.0	1.00	1.00
Totals	139	38.0	—	10	32.3	—	—

^aNISP and MNE values are presented in Table 1. Ratios calculated as: NISP - N whole / MNE - N whole (after Lyman 1994b:296).

Roost pitted and polished leporid remains are identified simply as partially digested bone. I acknowledge the effects of these and other taphonomic processes by employing discretion in attributing leporid bone attrition solely to eagle feeding.

Bone damage: Leporid crania and mandibles.—Most of the skull portions (NISP = 9) are maxillae with intact alveoli containing molars. The elements are usually separated at sutures and exhibit no punctures or breakage indicative of golden eagle feeding. Ten mandibles are represented by intact anterior portions with broken ascending rami. Figure 2 shows examples of this damage on a sample of Cathedral Roost specimens and *Lepus* mandibles recovered from a golden eagle nest in central Nevada. This damage appears to be a common consequence of raptor feeding (see also Hockett 1989) and probably is produced while stripping the masseter muscle and/or breaching the occipital region to extract the brain. However, the ascending ramus is a thin, low density portion of the mandible (Lyman 1984, Lyman *et al.* 1992), thus similar breakage may be produced by any number of taphonomic processes. Other mandibular fragments from the roost include two intact coronoid processes retaining small portions of the ascending rami, and one masseteric fossa with a portion of the angle. Two additional specimens are horizontal ramus fragments where extensive digestive corrosion has exposed root apices along the ventral borders. These specimens may represent bones cast in eagle pellets, but the location and extent of digestive corrosion is comparable to damage on coyote scatological bone (Schmitt and Juell 1994:253).

Bone damage: Leporid front limbs and scapulae.—Humeri from the roost exhibit damage generated by split-line weathering, partial digestion, and golden eagle feeding.

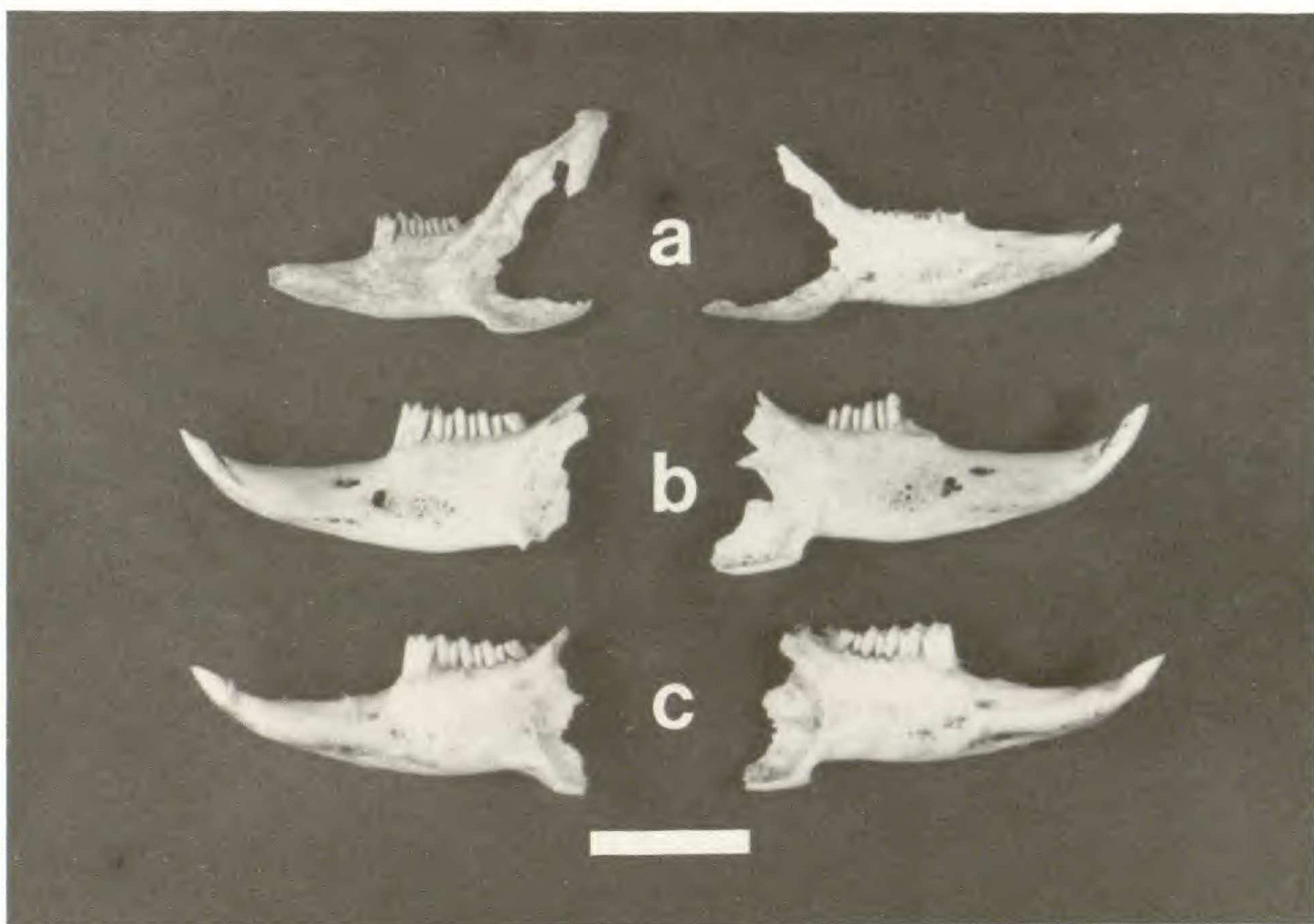


FIG. 2.—Lateral (buccal) view of leporid mandibles showing examples of ascending ramus damage produced by golden eagles. *Sylvilagus* sp., Cathedral Roost (a); *Lepus* sp., Cathedral Roost (b); *Lepus* sp., Railroad Valley, central Nevada (c). Bar scale is 2 cm in length.

Two cottontail proximal humerus fragments possess crushed shafts and localized rounding of fracture surfaces indicative of predator digestion. One jackrabbit proximal humerus possesses a small (2.6 mm diameter) aperture between the medial and lateral tuberosities, and a second (2.2 mm diameter) perforation on the opposing antero-medial surface just below the head. Damage location and morphology suggest that they were created by an eagle beak or talons (see also Hockett 1989, Livingston 1988:196–200). Five additional *Lepus* humeri are represented by distal ends retaining a few millimeters of shaft. These are relatively uniform in size (range = 17.0–22.7 mm; mean = 21.1 mm) and each displays transverse fractures that probably were produced by golden eagles; breakage morphology does not suggest the consequences of weathering. Barring longitudinal weathering fractures, the remaining humeri are complete and undamaged.

The modest assemblage of radii and ulnae largely contains whole, undamaged elements or nearly complete bones affected only by split-line exfoliation. One *Lepus* proximal ulna exhibits polish and pitting of the posterior margin of the olecranon process, traits common to scatological bone passed by Great Basin coyotes (Schmitt and Juell 1994:252–254). Fragmentary scapulae are represented by intact glenoid fossae retaining portions of the neck or neck/blade fragments. None displays breakage or punctures indicative of eagle feeding.

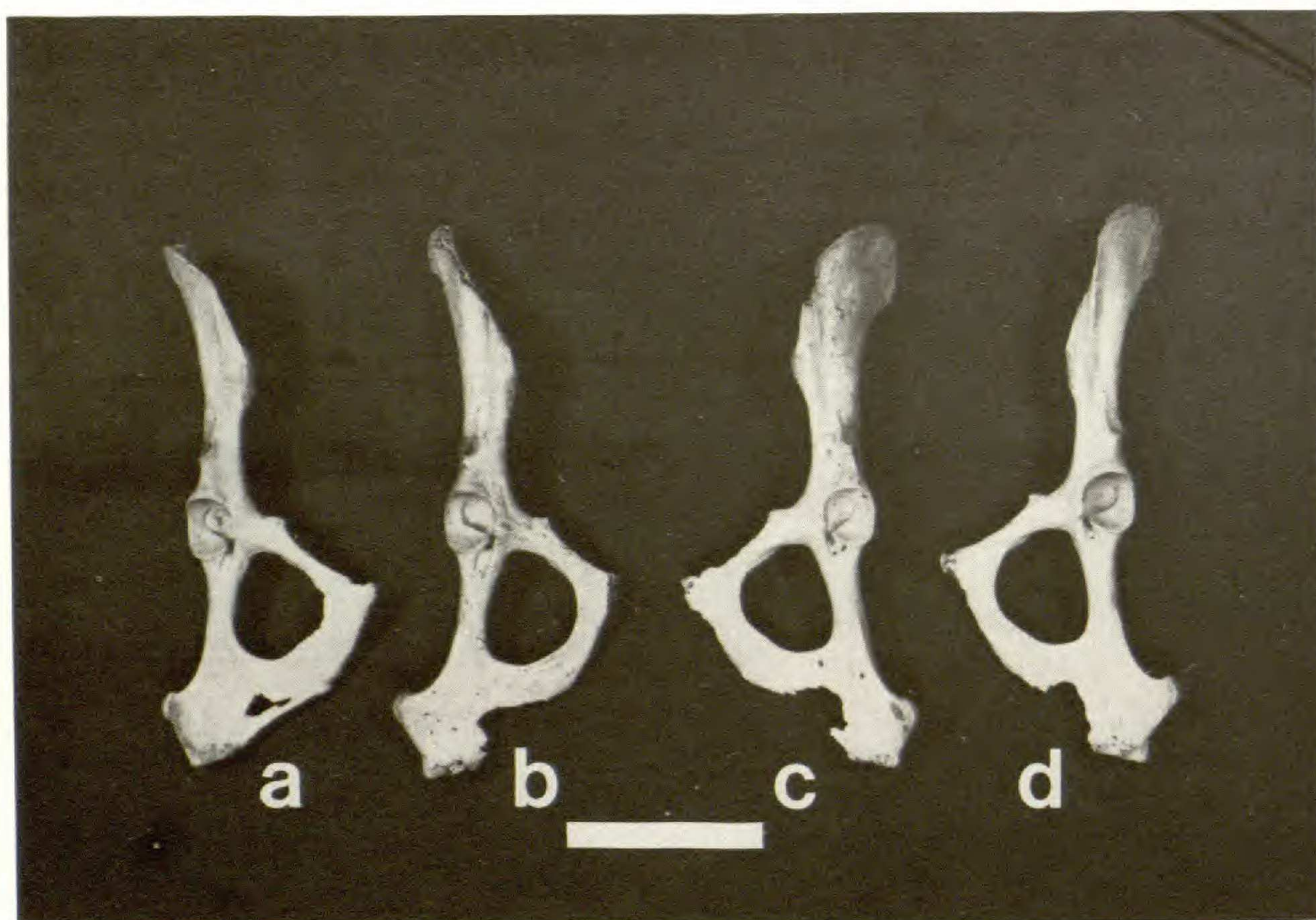


FIG. 3.—Anterio-lateral view of selected Cathedral Roost *Lepus* innominates showing examples of initial (a) and progressive stages (b-d) of weathering/bone loss along the ischiopubic ramus. Bar scale is 3 cm in length.

Bone damage: Leporid vertebrae, sacra, and innominates.—The vertebrae, sacra, and innominates are predominantly complete or nearly so, and none exhibits damage that can unequivocally be attributed to golden eagles. Most vertebra transverse and spinous processes and sacrum median crests are broken to some degree, but any number of taphonomic mechanisms are capable of damaging these thin, projecting segments. Each of the adult leporid innominates exhibits varying degrees of damage on the ischiopubic ramus. Attrition consists of localized bone removal of the posterior margin adjacent to the ischial tuberosity (Figure 3, b-d; NISP = 11) or breakage/removal of the ischiopubic ramus (NISP = 23; see also Hockett 1989: 128–129). Numerous superficial and deep muscles (e.g., adductor femoris, gracilis, and semimembranosus) are associated with the ischiopubic ramus and ischial tuberosity, and I suspect that golden eagles occasionally damage this portion of the pelvis while feeding on leporid carcasses. However, because the ischiopubic ramus is slender and the mineral density of this segment is low (Kreutzer 1992, Lyman 1984, Lyman *et al.* 1992), some may have been damaged by processes unrelated to golden eagle feeding (Schmitt 1994). Two Cathedral Roost specimens tend to support this inference as each possess small apertures formed by initial stages of weathering (Figure 3, a).

Twelve Cathedral Roost innominates also possess damaged ilia. Damage consists of transverse, jagged breakage just below (posterior) the iliac crest. As is the

case with many of the recovered limb bones, this attrition may have resulted from post-depositional weathering. The anterior ilium is a porous, low density segment (Lyman *et al.* 1992) and the "feathered" breakage of seven specimens appears to have resulted from prolonged exposure to the elements. However, five specimens are relatively unweathered and breakage is similar to the raptor "shearing" damage described by Hockett (1989, 1991). Hockett (1991, 1993) also reports the occurrence of beak/talon punctures behind the acetabular fossa in raptor-produced leporid assemblages, but no punctures occur in the large sample of innominates from Cathedral Roost. Finally, two cottontail innominate fragments are pitted and polished from partial digestion.

Bone damage: Leporid hind limbs.—Only four femora (6% of the NISP) exhibit damage that appears to have been inflicted by golden eagle feeding. The greater trochanter of one proximal femur is sheared off and is comparable to raptor damage described by Hockett (1991, 1993:121–122). A number of additional specimens display damage on their proximal ends, but attrition commonly is superficial and appears to reflect the initial stages of bone weathering. Three intact distal ends retain a few millimeters of shaft with transverse fractures. In these cases a comparison of breakage location and morphology with the numerous weathering fractures in the femora assemblage indicates breakage by a different taphonomic agent, possibly golden eagles. The remaining femora appear to have been deposited as complete bones that subsequently weathered and fractured, including one distal epiphysis which has sustained extensive rodent gnawing.

Golden eagle damage on tibiae includes punctures and fractures. Although numerous specimens have weathering breaks, two proximal fragments and five distal ends exhibit transverse fractures that are unlike the split-line weathering breaks observed elsewhere in the assemblage; these appear to have been generated by eagle feeding. One proximal fragment is unweathered and possesses a spiral break just below the anterior crest, and the other is a small (21 mm) intact proximal end retaining a few millimeters of shaft. The five distal fragments are relatively uniform in size (range = 22.6–27.4 mm; mean = 25.2 mm) and each exhibits jagged, transverse fractures of the distal shaft; one specimen was found articulated with the foot. Both raptors (Hockett 1989, 1993) and terrestrial carnivores (Andrews and Evans 1983, Schmitt and Juell 1994) are capable of snapping distal tibia shafts, therefore the Cathedral Roost specimens may have been fractured by golden eagles, scavenging carnivores, or both.

Localized damage on the medial surface of proximal tibiae has resulted from both golden eagle feeding and post-depositional weathering. Two specimens exhibit ovate, crushed apertures that appear to have been produced by a beak or talon (Figure 4, f). Nine additional specimens display varying types of damage in the same location, but most appear to have resulted from weathering. Five proximal ends exhibit early stages of weathering in the form of small pits exposing cancellous bone (Figure 4, a-b), and two display progressive weathering that resulted in the disintegration of part of the articular surface and anterior crest (Figure 4, d). A gouge on the proximal and lateral surface of one specimen resembles rodent gnawing (Figure 4, c) and the remaining specimen appears to have sustained a beak/talon puncture and subsequent weathering damage (Figure 4, e).

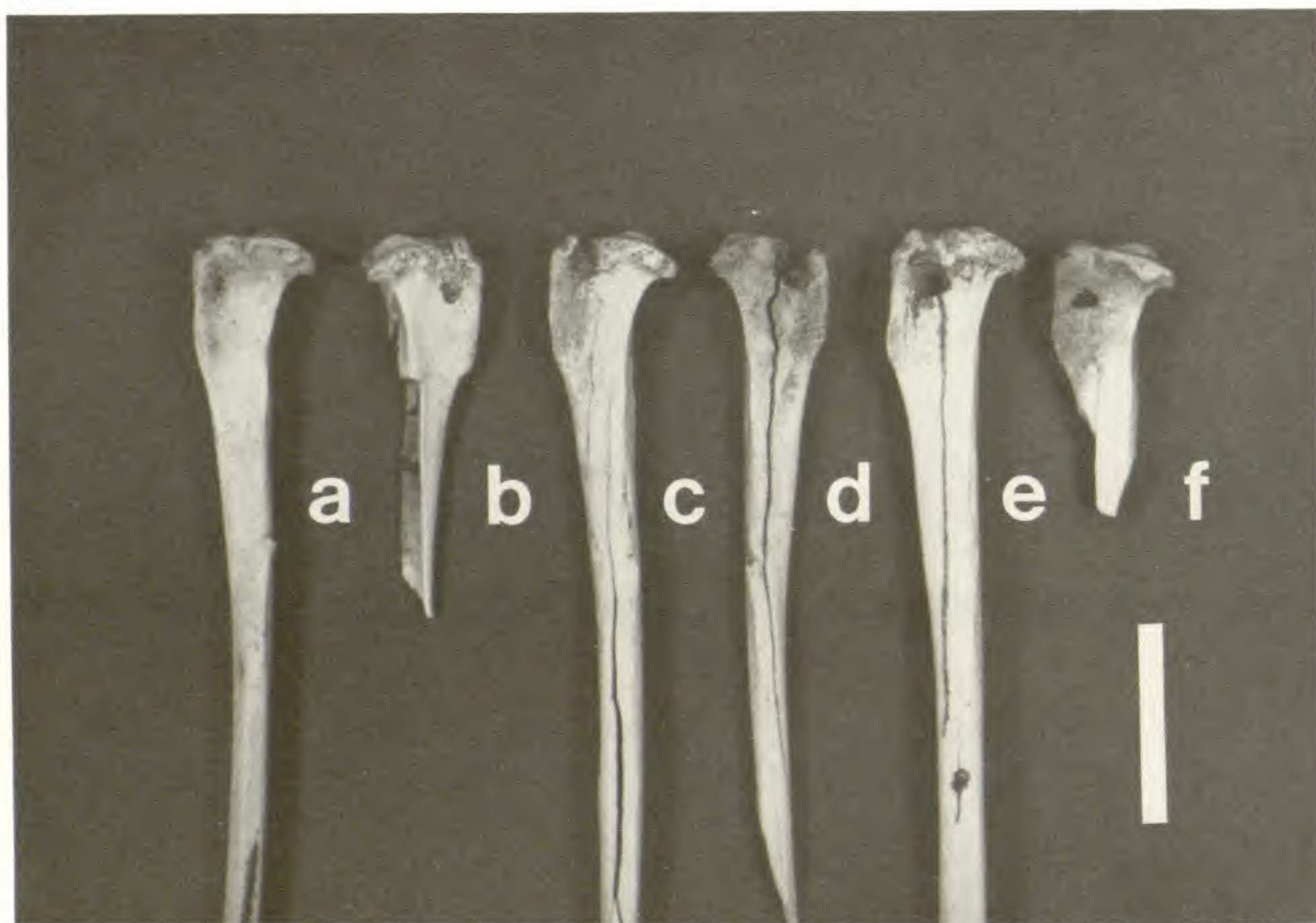


FIG. 4.—Damage on the lateral surface of selected proximal *Lepus* tibiae from Cathedral Roost; note also longitudinal weathering cracks/breakage. Initial pitting from weathering (a-b); rodent gnawing (c); progressive weathering (d); possible beak/talon puncture with subsequent weathering (e); beak/talon puncture (f). Bar scale is 3 cm in length.

Front and hind limb foot bones are abundant (Table 1) and most are complete. All of the carpals, tarsals, and astragali are complete and undamaged, and only seven phalanges (4.4%) are fragmentary. Forty-four (24%) of the *Lepus* metapodials are fragmented, including specimens splintered by advanced weathering and a few that display localized bone loss and overall polish that resulted from partial digestion. Calcanei are largely complete and undamaged (Tables 1 and 2), but two specimens also exhibit bone loss and corrosive attrition from predator digestion (Figure 5, b-c). The extent of corrosion suggests either that they passed through the stomach and intestines of a coyote or were subject to prolonged golden eagle digestion (see Hockett n.d.:Figure 3).

Evidence of bone attrition caused by golden eagles is extremely rare in the Cathedral Roost prey assemblage. Only three bones possess punctures that appear to have been inflicted by eagle beaks or talons. I am confident that breakage of the ascending rami and transverse fractures of some limb bones resulted from eagles feeding on prey carcasses, but other taphonomic mechanisms are capable of producing similar fractures (e.g., human subsistence activities or post-depositional trampling) and none of the bones exhibit attrition that can be attributed solely to golden eagles. While evidence for eagle-produced damage is scarce and often am-

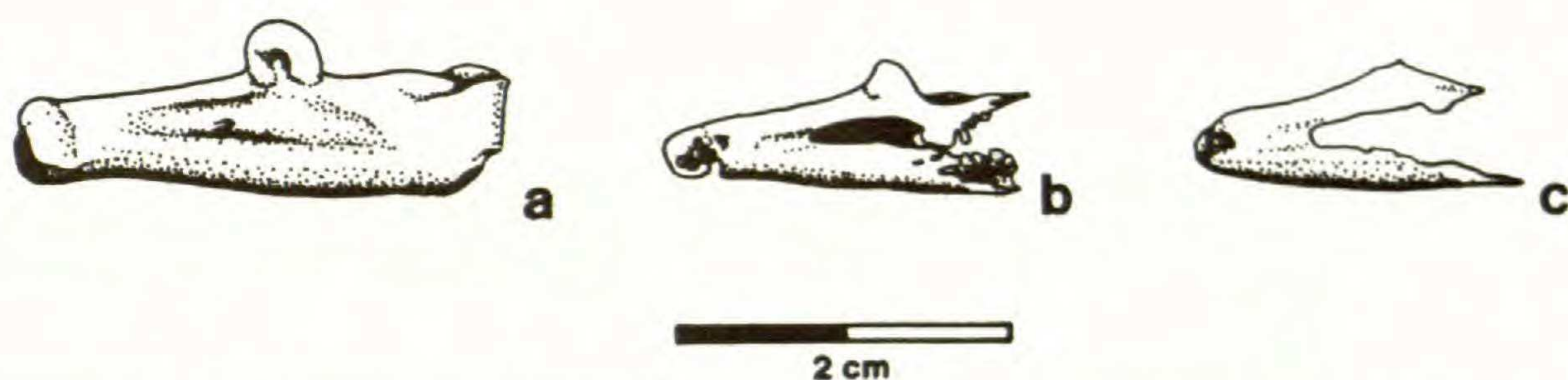


FIG. 5.—*Lepus calcani* from Cathedral Roost showing a complete, undamaged specimen (a) and corrosive attrition from partial digestion (b-c).

biguous, taxonomic abundances and body part frequencies may distinguish bone accumulations produced by golden eagles. To investigate this possibility, the Cathedral Roost assemblage is compared with golden eagle prey accumulations from another context.

PREY AND BODY PART FREQUENCIES: AN INTER-ASSEMBLAGE COMPARISON

Recently Hockett (1993, 1995) analyzed and reported leporid remains from Matrac Roost, a golden eagle nest in northwestern Nevada, thereby offering an exceptional collection to compare with the prey assemblage from Cathedral Roost. Matrac Roost is a single nest situated on a small ledge along the steep face of a bedrock ridge. The nest is approximately 10 m from the ground surface and overlooks the valley bottom. Hundreds of leporid remains were observed during 1990 field investigations and two golden eagle chicks along with three skinned and beheaded leporid carcasses were discovered in the nest in 1992 (Hockett 1993:106, 1995). Collections from the nest and vicinity yielded 930 leporid specimens (Hockett 1993:Table 6.3) representing both individual bones and articulated body parts. As with the Cathedral Roost assemblage, elements in articulated segments were isolated and tallied as single specimens. Hockett (1993:106–122) presents data on all of the skeletal remains collected from Matrac Roost, but his quantitative analyses focus on 12 major elements: crania (maxillae), mandibles, scapulae, humeri, radii, ulnae, innominates, sacra, femora, tibiae, astragali, and calcanei. The following comparisons employ only these 12 elements (see also Table 2).

The proportions of hare and cottontail bones recovered from Matrac Roost are similar to the Cathedral Roost assemblage. Identified jackrabbits from Matrac consist of 136 specimens representing a minimum of 130 elements, and the cottontail assemblage is comprised of 19 specimens representing an MNE of 17 (Hockett 1993:108). Most of the Matrac leporid remains are complete skeletal elements, especially foot bones (100%), radii (100%), and femora (80%). Matrac Roost contains higher proportions of juvenile *Lepus* elements (Hockett 1993:98) than Cathedral Roost (Table 1). Due to their limited size and transport capacity, prey assemblages produced by smaller raptors (e.g., northern harrier [*Circus cyaneus*] and barn owl [*Tyto alba*]) tend to be dominated by juvenile leporids (Hockett 1991). Golden eagles, however, are quite capable of capturing and carrying adult leporids (Eagle and Grubb 1986, McGahan 1968) and differences between the Matrac and Cathe-

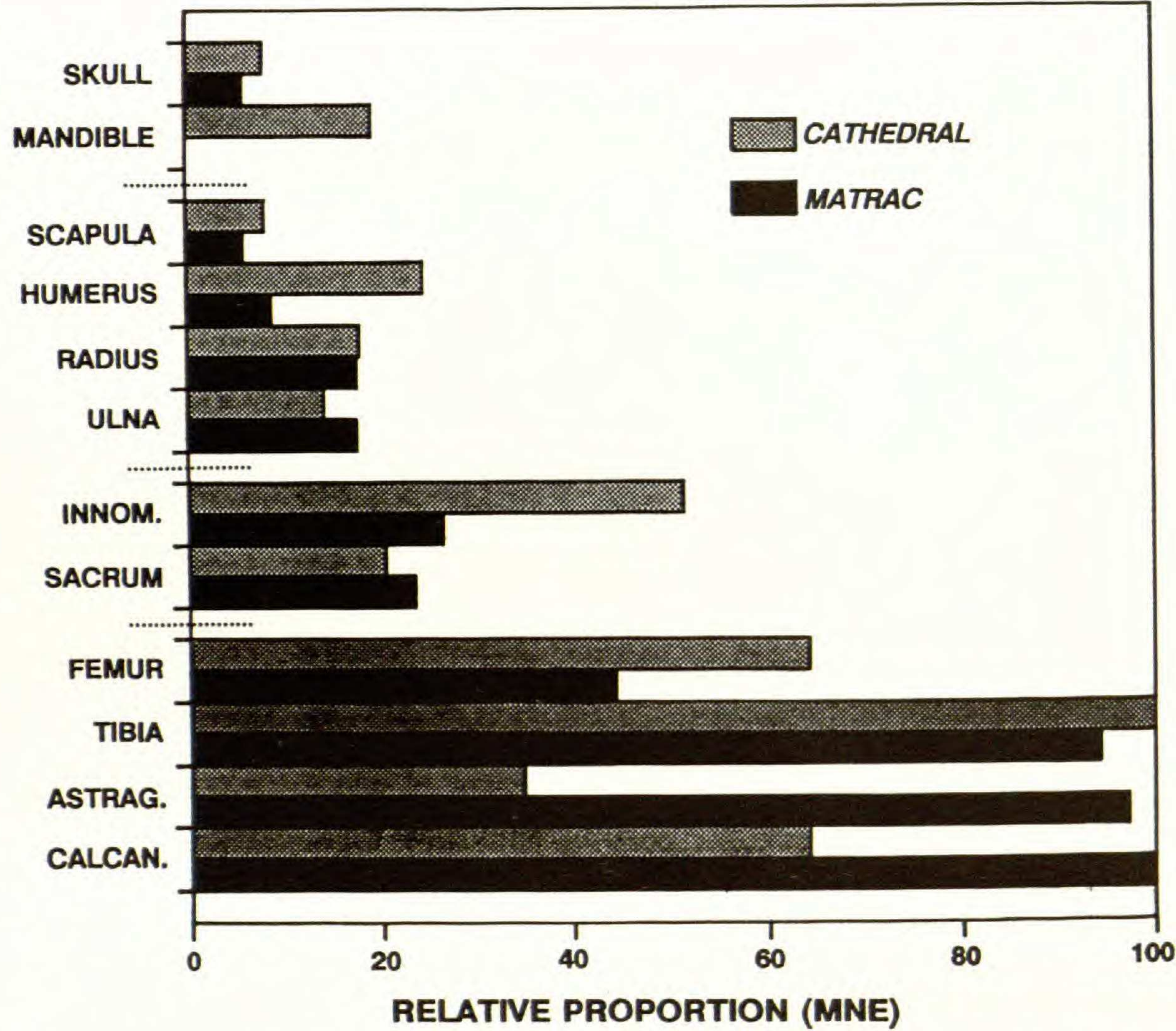


FIG. 6.—Relative proportions (MNE) of leporid elements recovered from Cathedral and Matrac roosts. Relative proportions for each aggregate are calculated as MNE/greatest MNE (Cathedral = 78 tibiae; Matrac = 34 calcanei [Hockett 1993: 108]) x 100. Dashed lines segregate gross body segments.

dral prey age structures likely reflect seasonal variation in the abundances and age structure of local prey populations rather than deliberate predator selection. Regardless, the high proportion of *Lepus* at Matrac Roost (88.4% of total MNE) corresponds with the proportion of *Lepus* recovered from Cathedral Roost (91.6%; Table 1). Although cyclical fluctuations in prey abundances may cause an increase in cottontail predation, jackrabbits characteristically dominate golden eagle diets in the Great Basin (Edwards 1969, Ryser 1985, Smith and Murphy 1979). The Matrac and Cathedral prey assemblages prove no exception.

Leporid body part representation at the two roosts also is markedly similar. Figure 6 presents the relative proportion of skeletal elements in each assemblage. Note that tibiae and associated foot bones are most common and front limbs and crania are rare (see also Edwards 1969:103). Innominates, sacra, and femora tend to be more abundant than forelimbs but they occur less frequently than tibiae. Variation in the proportion of these associated elements suggests that pelves (and some lumbar vertebrae), legs, and feet may have been brought to the roosts as articu-

lated segments on some occasions, but more often pelves and femora were stripped of flesh and abandoned and only the tibiae and articulated feet brought to the roosts as smaller, detached segments (see also Hockett 1993:113). The rank order abundances of the Matrac and Cathedral total leporid NISP values for the 12 major elements are positively correlated ($\tau = .605, p = .003$), as are the derived leporid MNE values ($\tau = .641, p = .002$). Comparing *Lepus* body part representation between the two aggregates also results in positive correlations for both NISP ($\tau = .678, p = .001$) and MNE ($\tau = .711, p < .001$). Regardless of the quantitative measure, these data suggest that golden eagle prey accumulations at Great Basin nest sites are dominated by hare remains characteristically comprised of high proportions of hindlimbs and low proportions of forelimbs and skulls. The next question is whether the homogeneity characterizing golden eagle prey accumulations is different from bone assemblages accumulated by other types of predators.

COMPARISONS WITH OTHER PREDATOR ACCUMULATIONS

A comparison of taxonomic and skeletal representation in the Cathedral Roost prey assemblage with those produced by other Great Basin predators reveals some rather pronounced differences. For example, Hockett's (1991) analyses of leporid bones from the Two Ledges barn owl pellets found cottontails (90.2% of leporid NISP) to be markedly more abundant than hares, high frequencies of anterior elements, especially humeri and mandibles, and high proportions of juvenile bones. Figure 7 illustrates differences between the proportions (NISP) of paired elements recovered from Cathedral Roost, Two Ledges barn owl pellets, and Great Basin coyote scats (Schmitt and Juell 1994). The rank order abundances of the Cathedral Roost and barn owl pellet (Hockett 1991:Table 1) leporid NISP are not correlated ($\tau = .18, p = .235$). Similarly, NISP:MNE ratios for the barn owl pellet leporid limb bones (i.e., humeri = 2.25, radii = 1.98, ulnae = 1.23, femora = 3.03, tibiae = 3.43; Hockett 1991:Tables 1 and 2) are larger and significantly different than the limb bone ratios at Cathedral Roost (Table 2: $X^2 = 218.69, df = 4, p < .001$).

Leporid assemblages produced by Great Basin coyotes also differ from eagle nest accumulations. Coyote food habits are similar to those of golden eagles in that both prefer to hunt jackrabbits, opportunistically pursuing both adults and juveniles, but body part representation (Figure 7) and bone attrition in coyote scat accumulations are often different. Although coyotes may leave body segments with little attached soft tissue at feeding loci, especially distal limbs with articulated feet (Andrews and Evans 1983, Schmitt and Juell 1994), they commonly consume the entire carcass. Furthermore, coyote scat assemblages will contain a more fragmentary and random array of body parts because they chew their prey. These assemblages will be dominated by high density segments because gastric acids will affect the survivorship of porous, low density segments (Schmitt and Juell 1994). Comparing leporid body part frequencies (NISP) of the ten paired elements from Cathedral Roost against leporid bone extracted from 40 coyote scats (Schmitt and Juell 1994:Table 4) results in an insignificant correlation ($\tau = -.09, p = .358$). Though coyote-generated scatological remains are conspicuously different than golden eagle prey bones stripped of flesh and deposited at nest sites, some corroded scat bones may be indistinguishable from eagle pellet bones

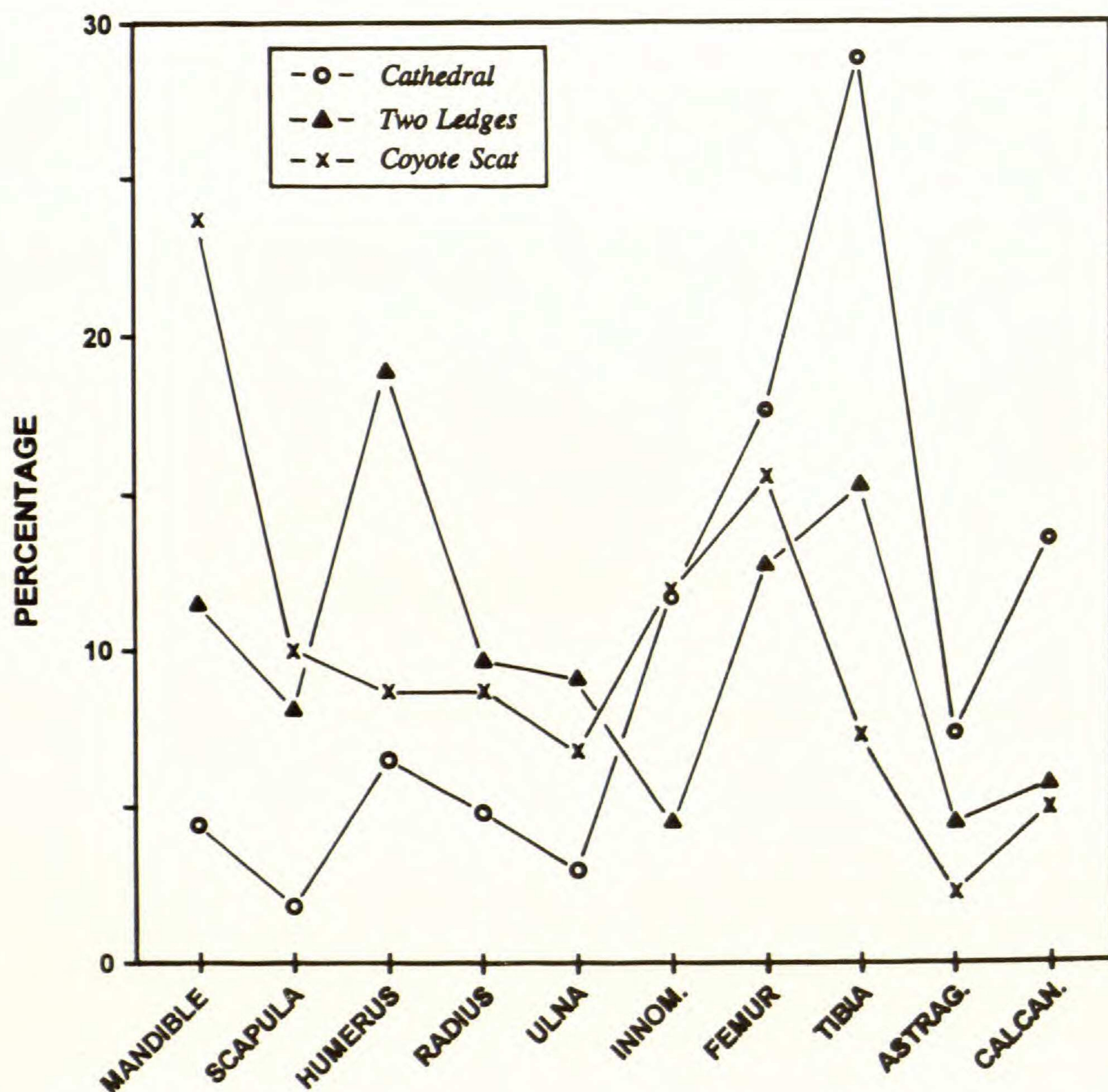


FIG. 7.—Percentage (NISP) of leporid paired body parts from Cathedral Roost (NISP = 367), Two Ledges barn owl pellets (Hockett 1991; NISP = 971), and Great Basin coyote scats (Schmitt and Juell 1994; NISP = 219).

(Hockett n.d.). In any case, “the presence of partially digested bone in an archaeological site will largely represent bones accumulated by non-human taphonomic agents” (Schmitt and Juell 1994:259), especially when represented by large leporid bone fragments.

Most important are the differences between golden eagle prey accumulations and human subsistence refuse. Great Basin ethnohistoric foragers used a variety of techniques to hunt hares and cottontails, including stalking or snaring individual prey, and procuring large numbers of individuals in communal drives (Downs 1966, Fowler 1992, Steward 1938). Given leporid body size and ethnographic descriptions of entire carcass utilization (Fowler 1989, Wheat 1967), the skeletal by-products of Great Basin human subsistence activities probably will contain a more

even distribution of body parts than those accumulated by golden eagles (see also Schmitt and Lupo 1995). Carcasses commonly were roasted on coals or dried and pounded for soup and bone meal (Downs 1966; Fowler 1989, 1992; Steward 1941; Wheat 1967). In some instances the ends of jackrabbit tibiae were broken off for marrow removal and subsequent manufacture of bone beads (Hockett 1994, 1995; Schmitt 1988, 1990). As a result, leporid skeletal element completeness and body part representation in golden eagle nest accumulations should differ from the fragmentary and/or burned bone assemblages customarily generated by human subsistence activities.

SUMMARY

The Cathedral Roost faunas provide data for distinguishing golden eagle prey accumulations in archaeological and paleontological contexts. Taxonomic and body part representation and skeletal element completeness offer the most reliable resolution, especially when considered together. Jackrabbits are the dominant prey species at nest sites and their skeletal remains are represented predominantly by posterior body segments, especially tibiae and foot bones. Comparison of the Cathedral Roost prey remains with leporid accumulations from a modern roost in Nevada disclosed marked similarities in taxonomic and skeletal element representation, and aspects of these assemblages were found to differ from prey remains accumulated by other predators. Golden eagle nests in the Great Basin are most often situated along steep craggy cliffs and canyon walls. As a result, prey assemblages will tend to accumulate at the base of cliffs, especially in associated caves and rock shelters (see Elston and Budy 1990), but they also may occur below trees used as perches or nest sites in mountains and valley foothills. Evidence of leporid skeletal attrition produced by eagle capture and/or feeding is rare; except for beak or talon punctures, bone damage alone will seldom distinguish golden eagle prey accumulations. The majority of the Cathedral Roost bones were complete and undamaged when deposited (often in articulated body segments) where they were subject to subsequent modification, especially split-line weathering. Bone weathering may have masked or erased a few additional punctures or fractures caused by golden eagle feeding, and some eagle-damaged bone may have been scavenged by local avian and mammalian predators and deposited elsewhere. Conversely, it is possible that some of the few partially digested specimens represent prey deposited by other predators. Although I am confident that the majority of the leporid remains were accumulated by eagles inhabiting the roost, the presence of rodent gnawing, bone weathering, and probable coyote scatological bone and bone scavenging provide testimony to the complex taphonomic mechanisms that can rapidly affect virtually any bone assemblage.

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